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CHANGES IN THE ANNUAL CYCLE OF NORTH AMERICAN RAPTORS ASSOCIATED WITH RECENT SHIFTS IN MIGRATION TIMING

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Abstract.—Recent changes in the timing of spring migration associated with climate change are occurring in hundreds of species of Northern Hemisphere birds. Much less is known about effects on autumn migration, especially for birds of prey. I studied simultaneous changes in spring and autumn phenology using data from 14 raptor species at two bird observatories on the shore of Lake Superior, North America. Median migration date advanced by 0.13 days·year^{-1} in spring and was delayed by 0.23 days·year^{-1} in autumn, with significant heterogeneity among species. Long-distance migrants were observed late in spring and early in autumn and showed less phenological change during autumn than short-distance migrants. The migratory period has become more extended, especially for short-distance migrants. Opposite responses during the two seasons had the effect of extending time spent to the north of the study area, by up to 30 days in some species since the early 1970s. These phenological shifts—potentially related to climate change—are causing dramatic changes in the annual cycle of North American raptors; whether these are beneficial or detrimental is unknown.
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Key words: annual cycle, climate change, hawk watch data, migration, phenology, raptors.

Cambios en el Ciclo Anual de Aves Rapaces Norteamericanas Asociados con Cambios Recientes en el Momento en que Realizan la Migración

Resumen.—Cambios recientes en el momento en que se realiza la migración de primavera asociados con el cambio climático están ocurriendo en cientos de especies de aves del Hemisferio Norte. Se sabe mucho menos acerca de los efectos sobre la migración de otoño, especialmente para aves de rapiña. Estudié los cambios simultáneos en la fenología de primavera y otoño usando datos de 14 especies de aves rapaces en dos observatorios de aves en la cosa de Lake Superior, Norteamérica. La mediana de la fecha de migración se adelantó 0.13 días por año en primavera y se retardó 0.23 días por año en otoño, y existió una heterogeneidad significativa entre especies. Los migrantes de largas distancias se observaron más tarde en primavera y más temprano en otoño, y mostraron menos cambio fenológico durante el otoño, que los migrantes de cortas distancias. El periodo migratorio se ha hecho más largo, especialmente para los migrantes de cortas distancias. Las respuestas opuestas entre temporadas tuvieron el efecto de extender el tiempo que las aves pasan al norte del área de estudio; dicha extensión ha sido de hasta 30 días en algunas especies desde principios de los años setenta. Estos cambios fenológicos –potencialmente relacionados con el cambio climático – están causando cambios dramáticos en el ciclo anual de las aves rapaces norteamericanas, pero aún se desconoce si tales cambios son benéficos o perjudiciales.

Changes in the timing of spring migration in birds are among the best-known biotic effects of recent climate change (Parmesan and Yohe 2003, Parmesan 2006). Long-term time series on the dates of passage of migratory birds have now been published from >90 localities (Lehikoinen and Sparks 2010). These data show that spring migration in the Northern Hemisphere is occurring nearly a week earlier than it was 30 years ago and that changes are most pronounced in species that migrate relatively short distances between their breeding and wintering grounds (Butler 2003, Lehikoinen et al. 2004). The few studies of autumn migration indicate weaker and more variable change (Jenni and Kéry 2003, Thorup et al. 2007, Van Buskirk et al. 2009).

Isolated analyses of phenological shifts in spring or autumn migration provide a limited picture of larger modifications in the avian annual cycle. Studies that include data on more than one point in the life cycle highlight potentially important changes in the timing of events in relation to one another. One well-known case is the duration of the interval between spring arrival and the onset of egg laying in the Pied Flycatcher (*Ficedula hypoleuca*), which shrank from ~20 days in 1980 to ~10 days in 2000 (Both

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and Visser 2001, Both et al. 2005). Van Buskirk et al. (2009) also documented correlated shifts in the timing of spring and autumn migration in numerous North American passerines, such that species with the most strongly advanced spring migration also exhibited delayed autumn migration. These are only two examples, but they suggest more complex effects of climate change than has been generally appreciated.

Here, I present results from two long-term surveys of spring and autumn migration timing of raptors in the Lake Superior basin of North America. My main focus is on changes in the relative timing of migration in the two seasons, and I argue that this reflects shifts in the amount of time spent in summering and wintering areas. In addition, the study provides information on changes in migration for a set of species that has been relatively little studied. Recent reviews of the timing of avian migration find that raptors are poorly represented among the several hundred species that have been studied so far (Lehikoinen and Sparks 2010, L. Bitterlin and J. Van Buskirk unpubl. data). Exceptions include two studies of European raptors that reported that most species are migrating earlier in autumn (Filippi-Codaccioni et al. 2010, Lehikoinen 2011) and one study that described no clear trends in spring first arrival date for six North American species (Murphy-Klassen et al. 2005).

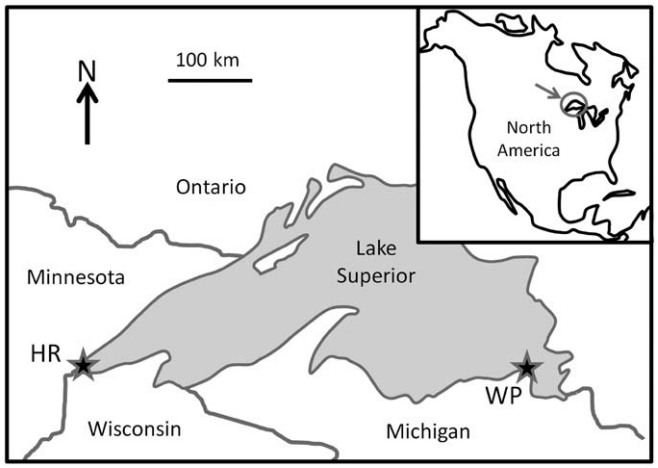

Fig. 1. Map of Lake Superior, indicating the locations of Whitefish Point Bird Observatory (WP) and Hawk Ridge Bird Observatory (HR). The arrow on the inset map indicates the location of Lake Superior within North America.

Methods

Data collection.—The data come from two raptor-migration observation sites on the edge of Lake Superior, North America (Fig. 1). Whitefish Point Bird Observatory (46.771°N, 84.957°W), operated only in spring, is located on the southern edge of the lake at the tip of a peninsula that concentrates birds moving north. Raptors are counted as they pass overhead from a platform at ground level. Hawk Ridge Bird Observatory (46.847°N, 92.032°W) is located at the westernmost point of Lake Superior, along a ridge that collects birds moving along the southwest-oriented edge of the lake during autumn migration. The observation site is along the crest of a ridge, and raptors sometimes pass at or below eye level. At both locations, raptors are counted each day by variable numbers of volunteers, directed by at least one experienced observer. The dates and hours of observation for the two sites have remained remarkably constant over the past 30 years (about 15 March to 31 May at Whitefish Point and 15 August to 30 November at Hawk Ridge). Exact dates are in supplementary Table S1 (online; see Acknowledgments). Whitefish Point averages 7.5 h of operation per day, with no trend through the years. Hawk Ridge averages 6.9 h of operation per day, with increasing effort in recent years (Table S1). These two sites were chosen for this study because

Table 1. List of species included in the study, abbreviations used in the figures, and average (*n*, with SD in parentheses) of the number of birds observed per year.

Species	Abbreviation	Migration distance	Spring		Autumn	
			Years	*n* (SD)	Years	*n* (SD)
Turkey Vulture (*Cathartes aura*)	TUVU	Long	34	223.2 (159)	40	901.2 (521)
Osprey (*Pandion haliaetus*)	OSPR	Long	34	110.1 (44)	40	257.0 (143)
Bald Eagle (*Haliaeetus leucocephalus*)	BAEA	Short	34	209.3 (175)	40	1,673.5 (1,746)
Northern Harrier (*Circus cyaneus*)	NOHA	Short	34	357.8 (174)	40	445.4 (236)
Sharp-shinned Hawk (*Accipiter striatus*)	SSHA	Short	34	9,205.6 (4,716)	40	12,965.6 (4,593)
Cooper's Hawk (*A. cooperii*)	COHA	Short	33	60.6 (35)	40	93.0 (77)
Northern Goshawk (*A. gentilis*)	NOGO	Short	34	75.9 (46)	40	642.3 (976)
Broad-winged Hawk (*Buteo platypterus*)	BWHA	Long	34	4,813.0 (2,854)	40	39,185.1 (28,163)
Red-tailed Hawk (*B. jamaicensis*)	RTHA	Short	34	1,916.7 (1,304)	40	6,172.8 (3,299)
Rough-legged Hawk (*B. lagopus*)	RLHA	Short	34	749.2 (558)	40	345.9 (227)
Golden Eagle (*Aquila chrysaetos*)	GOEA	Short	33	44.3 (29)	40	72.5 (71)
American Kestrel (*Falco sparverius*)	AMKE	Long	34	477.0 (206)	40	1,298.2 (812)
Merlin (*F. columbarius*)	MERL	Short	32	76.9 (39)	40	131.2 (107)
Peregrine Falcon (*F. peregrinus*)	PEFA	Long	32	33.2 (19)	38	45.1 (34)

they are long-running, follow well-standardized methods and observation effort, are within the same geographic region, and sample the same set of common species.

Daily counts for each species (1979–2012 for Whitefish Point and 1972–2011 for Hawk Ridge) were downloaded from a website maintained by the Hawk Migration Association of North America (see Acknowledgments). I also contacted the scientific coordinators of both observatories to ensure that the data were accurate and complete.

I studied the 14 species that were observed in ≥15 years, and included all years in which ≥5 individuals of the species were observed. Table 1 lists names and sample sizes of these species. Although the Red-shouldered Hawk (*Buteo lineatus*; all other scientific names are given in Table 1) was frequent at Hawk Ridge during the early years, this species was not included here because ≥5 individuals were observed only once within the past 12 years.

Statistical analyses.—There were two stages in the analysis. First, the timing of migration for each species was defined by the dates on which the first 10%, 50%, and 90% of individuals were observed. These three quantiles were calculated from a truncated normal distribution fitted to the data by maximum likelihood (Jenni and Kéry 2003). The truncation points were the first and last dates on which data were collected in that year, and the number of birds observed on each day was standardized by the hours of observation effort. Figure 2 illustrates three examples of fitting truncated normal distributions. This approach was necessary because the observation period did not encompass the entire migration period for all species, and there were a few years in which the observation period was abbreviated (Table S1). Truncation had little effect on the estimated mean passage date for species that migrate in the middle of the observation period, such as the American Kestrel and Sharp-shinned Hawk. But for species that migrate relatively early (e.g., the two eagles in spring) or late (e.g., Northern Goshawk in autumn or Peregrine Falcon in spring), the method indicates that the mean passage date would have been even earlier or later had the observation period been longer (Fig. 2 and supplementary Fig. S1).

In a second stage of analysis, I tested for directional changes in estimated passage date over the entire duration of the study. This was done by fitting two repeated-measures mixed-effects linear models, separately for spring and autumn. The response vector was defined by the dates on which the 10%, 50%, and 90% quantiles of migrants were estimated to have passed. These quantiles came from the fitted normal distributions, so the date of median passage (50% quantile) is also the mean passage. Both models contained the fixed effects of quantile, year, migration distance, and their interactions. Migration distance was included because studies mentioned above indicated that the response to climate change has been stronger in short-distance migrants. It is not known whether this is true for raptors. Migration distance was a categorical variable because there is a distinction between long-distance migrants, which winter mostly south of North America, and short-distance migrants, which winter primarily in the United States (Poole 2008). The two models also contained random effects to estimate variation among species (included as random subjects), heterogeneity among species in their slopes on year, the covariance between these two, and variation among species

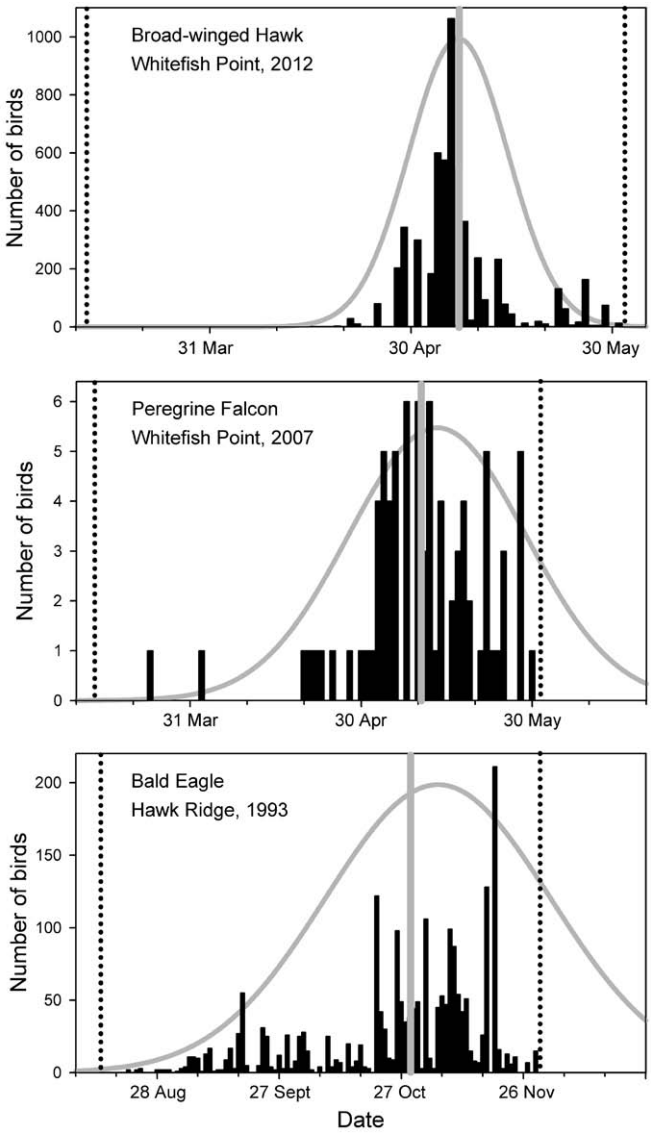

Fig. 2. Examples of truncated normal distributions fitted to HawkWatch data. The vertical dotted lines represent the first and last dates of observation. Black bars represent the observed number of birds per hour of observation (here multiplied by 10 and rounded to the nearest integer). The vertical gray line indicates the median date calculated from observed data. The gray normal curve, drawn on an arbitrary vertical scale, is the estimated truncated normal distribution. The top panel represents the usual situation in which most of the migratory period fell within the range of observation dates, so that the estimated distribution closely matched the observed data. The lower two panels represent cases in which the median passage date would have been later had the observation period been extended.

in differences among quantiles. The interpretation of random effects is described below and in supplementary Table S2, and their significance was determined by likelihood ratio (LR) tests. Observations were weighted by the natural logarithm of the number of individuals observed in that year. Including year as a linear

term was supported by results of preliminary segmented regressions carried out for each species separately (package 'segmented' in R; Muggeo 2003). On the basis of LR tests, a segmented model was preferred over simple linear regression for only one species in spring and no species in autumn. In both cases, model fit—as inferred from the pseudo-R^2 calculated as the squared correlation between fitted values from the model and observed values of the dependent variable (Anselin 1988)—was excellent (R^2 = 0.89 in spring; R^2 = 0.92 in autumn). Model-fitting was by REML in SAS, version 9.2, proc glimmix (SAS Institute 2010); the analysis code is available in Table S2.

Results

Across all species, the timing of 50% (median) passage became earlier in spring and later in autumn (Fig. 3). The average rate of change, estimated by the effect of year evaluated at the level of species, was nearly twice as high in autumn as in spring. Median migration was delayed by 2.3 ± 0.75 (SE) days decade^{-1} in autumn and advanced by 1.3 ± 0.26 days decade^{-1} in spring. Long-distance migrants were significantly later than short-distance migrants in spring, but significantly earlier in autumn (Fig. 3 and Table 2). The timing of migration of short-distance migrants in autumn shifted slightly more than that of long-distance migrants, as indicated by the interaction between year and migration distance in Table 2. No such difference occurred in spring. The marginally nonsignificant interaction between quantile and migration distance in both seasons indicated that, with some exceptions, long-distance migrants had shorter migration periods. For many species, both spring and autumn migration periods became more protracted over the decades. This was reflected in significant year × quantile interactions and a strong tendency for the 10% quantile to have more negative slopes of date regressed against year than the 90% quantile (Fig. 4 and Table 3). However, the three-way interaction indicated that—in spring at least—it was mostly short-distance migrants that extended the migration period; species that overwinter mostly south of North America continued to pass Whitefish Point relatively quickly in spring. The Broad-winged Hawk and American Kestrel have, if anything, shortened their spring migration period (Fig. 4). Supplementary Figure S2 (online) presents examples of long-term trends in migration timing for long-distance and short-distance migrants.

Large random effects of species in both seasons reflected considerable variation among species in phenology (Table 2 and Fig. 3). Significant heterogeneity across species in differences among quantiles meant that species varied in their duration of passage (see Fig. S2). There was also significant variability among species in their slopes of timing against year, especially in autumn. A positive covariance between random slopes and intercepts in autumn arose because the species that reacted most strongly were also late migrants. This is visible as a strong positive correlation in Figure 3B. The corresponding covariance term was negative but nonsignificant in spring, which indicates that late-migrating species shifted only slightly more strongly (Fig. 3A).

Simultaneous shifts in both spring and autumn phenology resulted in dramatic changes in the interval between the two migration phases (Fig. 5). This was especially true for species that migrate early in spring and late in autumn. The most extreme examples were the Bald Eagle, Golden Eagle, and Rough-legged Hawk, which increased the amount of time spent to the north of the study area by ~0.8 days year^{-1}. This amounts to a lengthening of the summer season by >1 month over the 40-year duration of the study.

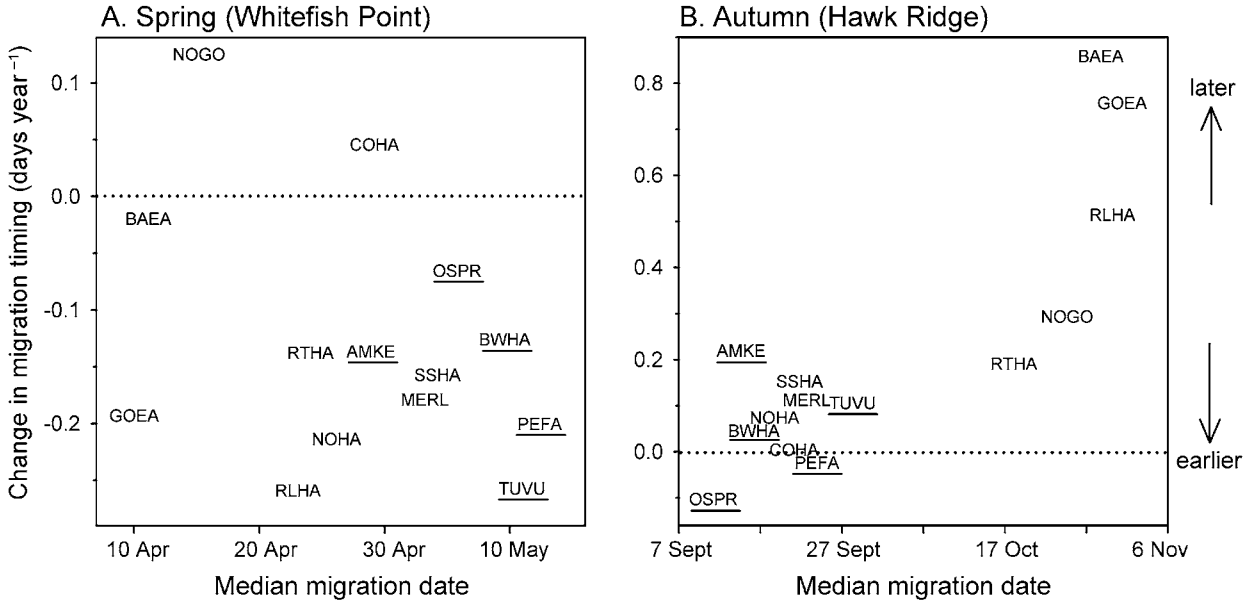

Fig. 3. Median migration passage date and change in the median date for raptors observed at HawkWatch sites on Lake Superior, North America, during spring and autumn. Observations are coded by species abbreviations, given in Table 1. Underlined species are long-distance migrants. Note that the axes are scaled differently in the two panels.

Table 2. Summary of models testing for changes in the timing of migration of raptors recorded at Whitefish Point (spring) and Hawk Ridge (autumn). For fixed effects, entries in the table are the estimated coefficient in units of days, with negative coefficients reflecting earlier migration dates, and the *F*-ratio; degrees of freedom (df) are based on Satterthwaite's approximation. For random effects, entries are variance components and likelihood ratio tests. Observations were weighted by the logarithm of the number of individuals observed. Significance tests for random effects and fixed effects with more than two levels correspond to the overall effect rather than coefficients for specific levels. Significant results are in bold.

		Spring				Autumn			
Source	Level	Estimate	Test statistic	df	*P*	Estimate	Test statistic	df	*P*
Fixed effects									
Intercept		135.3				307.5			
Quantile	10%	–45.63	**121.67**	**2, 24**	**0.0001**	–41.65	**78.64**	**2, 24**	**0.0001**
	50%	–22.81				–20.82			
Year		–0.049	**21.67**	**1, 11**	**0.0008**	0.471	**9.34**	**1, 12**	**0.0102**
Migration distance	long	6.64	**8.19**	**1, 12**	**0.0143**	–32.04	**10.09**	**1, 12**	**0.0080**
Quantile * year	10%	–0.302	**6.62**	**2, 1,350**	**0.0014**	–0.229	**9.16**	**2, 1,615**	**0.0001**
	50%	–0.151				–0.115			
Quantile * migration distance	10% long	12.92	3.31	2, 24	0.0536	14.04	3.23	2, 24	0.0570
	50% long	6.46				7.02			
Year * migration distance	long	–0.199	1.22	1, 11	0.2928	–0.377	**5.01**	**1, 12**	**0.0454**
Quantile * year * migration distance	10% long	0.270	**4.33**	**2, 1,350**	**0.0134**	0.151	2.23	2, 1,615	0.1081
	50% long	0.135				0.076			
Random effects									
Species (intercepts)		57.5	**768.9**	**1**	**0.0001**	195.3	**1,833.3**	**1**	**0.0001**
Quantile * species		41.7	**530.1**	**2**	**0.0001**	51.0	**765.5**	**1**	**0.0001**
Year * species (slopes)		0.006	**5.2**	**1**	**0.0224**	0.059	**161.6**	**1**	**0.0001**
Covariance between intercepts and slopes		–0.217	0.7	1	0.4103	2.795	**10.8**	**1**	**0.0010**

Discussion

The changes in timing of migration observed in the present study are broadly compatible with earlier work. For spring migration, the data agree with a pattern of earlier passage in recent years observed in many birds in the Northern Hemisphere (Lehikoinen et al. 2004, Lehikoinen and Sparks 2010). The results for autumn also confirm the very heterogeneous findings reported in this season for other species (Jenni and Kéry 2003, Van Buskirk et al. 2009), although they also suggest that raptors are delaying autumn migration more than other groups of birds (Lehikoinen and Sparks 2010). In some cases, differences among species may be interpretable in terms of their natural history. For example, the Rough-legged Hawk and Golden Eagle exhibited very strong shifts in phenology, and these species breed at the high latitudes that are most affected by recent climate warming (Overpeck et al. 1997, IPCC 2007). The Northern Goshawk, by contrast, showed little long-term change in timing of migration. This species is especially sensitive to the density of medium-sized prey, and as a result its phenology may be determined by food supply rather than climate (Mueller et al. 1977, Salafsky et al. 2007). The modest changes observed in long-distance migrants are consistent with data from other groups of birds (Lehikoinen et al. 2004). The explanation has been that, because these species overwinter in tropical regions, they are unaware of conditions to the north and therefore cannot adjust their phenology appropriately (Lehikoinen et al. 2004). It has also been argued that the phenology of long-distance migrants is governed by day length rather than weather conditions (Berthold 1996, Gwinner 1996).

As in earlier work, these data provide no direct evidence that phenological shifts are caused directly by climate change. However, many other studies have noted correlations between the changes in migration phenology and concurrent changes in local or regional conditions (usually temperature and North Atlantic Oscillation; e.g., Cotton 2003, Hüppop and Hüppop 2003, Marra et al. 2005, Gordo 2007). More convincingly, detrended fluctuations in timing of migration in some species are closely associated with detrended fluctuations in climate (Saino et al. 2007, Van Buskirk et al. 2009). It therefore seems plausible to suggest a mechanism involving the reactions of individual birds to gradual changes in the conditions experienced before and during migration.

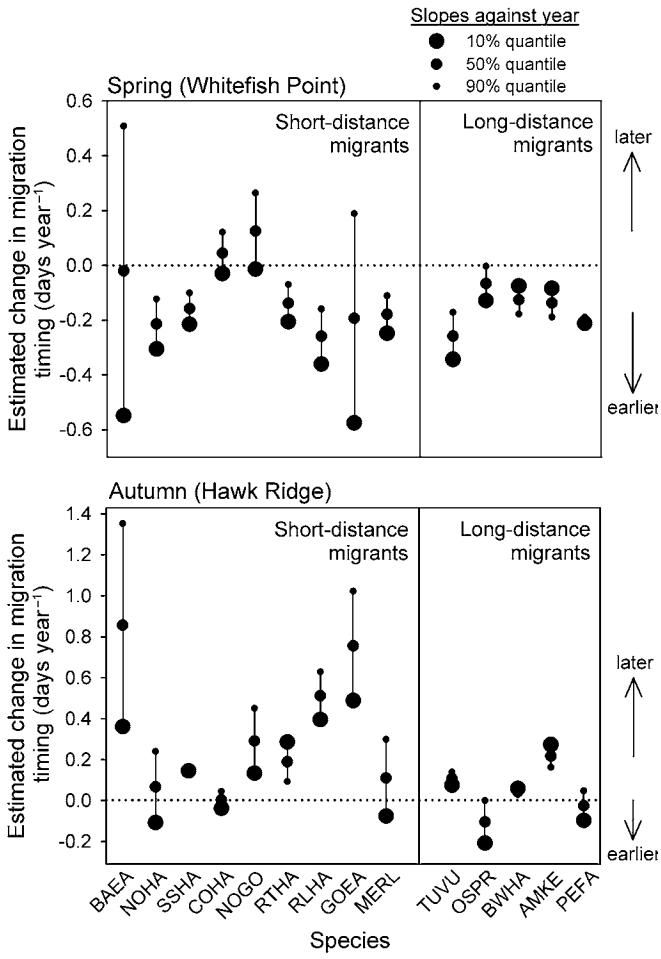

Fig. 4. Slopes estimated by regression of migration timing against year for 14 raptor species sampled in spring and autumn on Lake Superior. Vertical lines connect estimates from three separate regressions on the 10%, 50%, and 90% quantiles of the distribution of migrants for each species. Values below zero indicate that birds are migrating earlier in recent years. Species abbreviations are given in Table 1. Standard errors of the slopes shown here are given in Table 3.

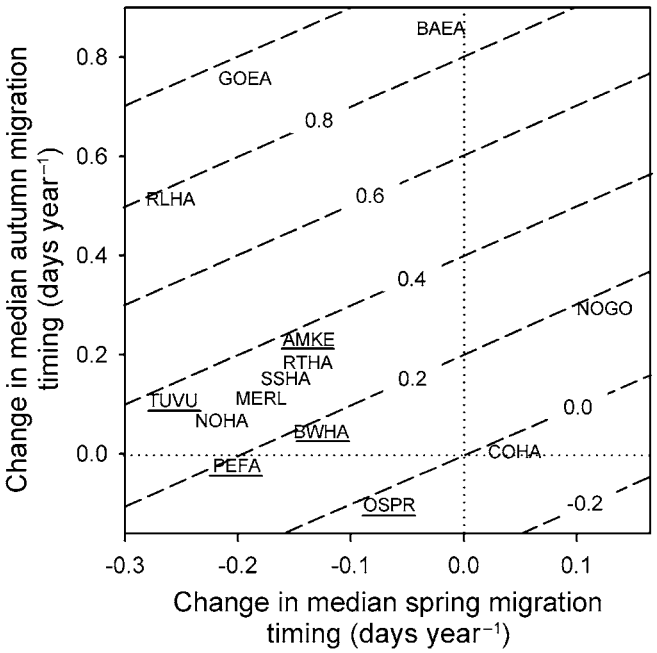

Fig. 5. Long-term change in the duration of the breeding season, estimated by the interval between the median passage date of spring and autumn migrants, for 14 raptor species sampled on Lake Superior. Dotted lines represent a slope of zero (i.e., no change in timing). Dashed contour lines are the change in the interval between spring and autumn migration (days year^{-1}). Species abbreviations are defined in Table 1, and underlined species are long-distance migrants. For three species (Bald Eagle, Rough-legged Hawk, and Golden Eagle), the duration of the summer season has increased by ~0.8 days year^{-1}.

Whatever the causal mechanism, some species are experiencing potentially important modifications in the annual cycle, because spring and autumn migrations are shifting in opposite directions. Since observations began in the 1970s, the interval between spring and autumn migrations has increased by ~30 days for the Bald Eagle, Rough-legged Hawk, and Golden Eagle. For the majority of species in the present study, changes are in the range of 0.2–0.4 days year^{-1}, but even these modest values imply that the inter-migration interval has lengthened by 1–2 weeks in just a few decades. This likely reflects an increase in the time spent in residence on or near the breeding area (Thorup et al. 2007), but there are other possibilities. For example, the rate of movement during migration may have changed or the birds may have shifted the locations of their winter or summer ranges (Marra et al. 2005, Lehikoinen and Sparks 2010). Regardless of the specific cause, these species are spending more time to the north of Lake Superior than they used to, and less time to the south. Of course, this conclusion assumes that Whitefish Point and Hawk Ridge sample comparable raptor populations. In fact, the species composition is very similar between sites, reflected by the positive correlation in an index of species abundance (r = 0.66, P = 0.01, n = 14; Farmer and Smith 2010). More importantly, long-term trends in abundance detected by the two sites are highly correlated at the level of species (r = 0.73, P < 0.01, n = 14).

These results suggest that raptors perceive the relative qualities of their summer and winter habitats differently than passerines. For the latter, spring migration has consistently become earlier, and there has been no consistent change—or species-specific changes—in autumn (Jenni and Kéry 2003, Lehikoinen and Sparks 2010). The usual interpretation is that passerines attempt to reach the breeding area in spring as early as possible, and indeed there is evidence for natural selection favoring early reproduction in many birds, including many nonpasserines (Newton 2008). But passerines seem to depart for their wintering areas as soon as breeding is finished, such that autumn migration is not generally delayed. On average, there has been no change in the breeding-area residence time (Thorup et al. 2007, Van Buskirk et al. 2009). That climate change has prompted delayed autumn departure as well as advanced spring arrival in raptors implies that breeding habitats, or at least northern regions, are preferred over

Table 3. Coefficients from regressions of migration date against year for spring migration at Whitefish Point and autumn migration at Hawk Ridge. Dates for the 10%, 50%, and 90% quantiles come from truncated normal distributions fit to the numbers of individuals per hour of observation for each species in each year. Regressions were weighted by the natural logarithm of the sample size. Entries in the table are the slope (SE), in days year^{-1}; coefficients that differ significantly from zero are in bold.

	Spring migration (Whitefish Point)			Fall migration (Hawk Ridge)		
Species	10% quantile	50% quantile	90% quantile	10% quantile	50% quantile	90% quantile
Turkey Vulture	**–0.343 (0.090)**	–0.258 (0.134)	–0.172 (0.214)	0.075 (0.058)	**0.107 (0.015)**	**0.140 (0.051)**
Osprey	**–0.129 (0.060)**	–0.066 (0.073)	–0.003 (0.125)	**–0.208 (0.048)**	**–0.104 (0.034)**	0.001 (0.039)
Bald Eagle	**–0.548 (0.193)**	–0.020 (0.114)	**0.508 (0.149)**	**0.361 (0.160)**	**0.857 (0.128)**	**1.353 (0.257)**
Northern Harrier	**–0.305 (0.096)**	**–0.214 (0.087)**	–0.123 (0.109)	–0.107 (0.138)	0.067 (0.080)	**0.240 (0.073)**
Sharp-shinned Hawk	**–0.215 (0.080)**	**–0.158 (0.058)**	–0.101 (0.072)	**0.146 (0.050)**	**0.151 (0.038)**	**0.157 (0.049)**
Cooper's Hawk	–0.030 (0.120)	0.045 (0.112)	0.121 (0.421)	–0.038 (0.077)	0.004 (0.064)	0.045 (0.080)
Northern Goshawk	–0.014 (0.222)	0.125 (0.141)	0.264 (0.147)	0.134 (0.120)	**0.292 (0.116)**	**0.451 (0.164)**
Broad-winged Hawk	–0.075 (0.072)	–0.126 (0.084)	–0.178 (0.121)	0.059 (0.049)	0.044 (0.032)	0.029 (0.038)
Red-tailed Hawk	–0.206 (0.123)	–0.138 (0.116)	–0.070 (0.191)	**0.287 (0.107)**	**0.190 (0.078)**	0.093 (0.112)
Rough-legged Hawk	**–0.360 (0.099)**	**–0.259 (0.081)**	–0.159 (0.125)	**0.396 (0.103)**	**0.513 (0.111)**	**0.629 (0.142)**
Golden Eagle	**–0.575 (0.240)**	–0.193 (0.169)	0.189 (0.132)	**0.489 (0.082)**	**0.756 (0.108)**	**1.023 (0.168)**
American Kestrel	–0.084 (0.075)	**–0.137 (0.065)**	–0.189 (0.097)	**0.274 (0.074)**	**0.218 (0.053)**	**0.163 (0.052)**
Merlin	–0.248 (0.146)	–0.179 (0.096)	–0.111 (0.125)	–0.076 (0.097)	0.111 (0.069)	**0.299 (0.073)**
Peregrine Falcon	**–0.212 (0.084)**	**–0.201 (0.063)**	–0.190 (0.105)	–0.097 (0.076)	–0.025 (0.051)	0.048 (0.067)

wintering habitats by these species. It may be that competition on the wintering area is more severe, as suggested by relatively high raptor densities and species richness in winter (e.g., Boano and Toffoli 2002, Ferguson 2004). There is some evidence that survival of raptors is lower during migration and in winter than in the summer range (Harmata et al. 1999, Newton et al. 1999, McIntyre et al. 2006). Although they would not necessarily survive better if they remained longer on their summer range, delaying migration may nevertheless enable birds to remain longer in a more favorable part of their geographic distribution.

Most studies of biotic responses to changing climate emphasize negative effects on individuals and populations. Indeed, there is evidence that avian phenological changes are at least sometimes associated with reduced performance of individuals (Both and Visser 2001, Both et al. 2005) or declines of populations (Jones and Cresswell 2010). However, the longer interval between spring and fall migrations that I have detected could have positive implications for raptors. Delayed autumn departure would provide birds with a protracted post-breeding period to prepare for migration, which would enable juveniles, in particular, an opportunity to reach better condition by the time they depart for the south. Delayed breeding and a shortened post-breeding period can be associated with delayed migration in some birds (Mulvihill et al. 2009, Stutchbury et al. 2011). In addition, altered migration schedules may allow birds to spend more time feeding in stopover areas (Bairlein and Hüppop 2004) or may enable them to exploit only the best weather conditions for travel (Jenni and Schaub 2003). Both of these should lead to improved survival during migration and during the winter and suggest that behavioral responses to climate change may quite often be beneficial (Van Buskirk 2012).

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